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The Simplest Model of Targeted Migration

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A simple model of targeted migration is studied. The model implies the global information access of the beings migrating from station to station. This approximation yields a special class of models which generater a semi-group. Various dynamic regimes, as well as the stability conditions are studied. Some further expansions of the modelling based on evolution optimality principle are considered.

Keywords: optimality, selection, projection, maximization, stability, information.

Introduction

Modelling of the dynamics of biological communities is essential tool for their studies. The fundamental works by V. Volterra [1, 2] made outstanding start-up of mathematical ecology and mathematical modelling of population dynamics (see also [3, 4]). This model follows, in brief, a chemical kinetics, with a population being a kind of chemical reactor, where various "chemical" reactions take place. Reproduction, death and other types of interaction of organisms are supposed to be these reactions.

One should avoid flattering with the (reasonable, or even good) coincidence of the solutions of such "reaction – diffusion" systems to observations of "real" dynamics of some populations and communities. The point is that the diversity and abundance of possible (structurally stable) regimes of such dynamic systems exceed drastically any really available family of trajectories of real systems. Thus, one always is able to match a differential equation (or a system of differential equation, either ordinary, or partial differential equations) to the dynamic behavior of any really observed system. Doubtlessly, living organisms, even microorganisms, differ drastically in their "microscopic" behavior from the chemical substances and relevant chemical reactions.

Vito Volterra, the founder of the mathematical biology of populations understood pretty well this discrepancy. Later, the comprehension of limitations of this chemical methodology fell off. The situation is going worse when one tends to model a dynamics of spatially distributed populations and communities. Basically, "reaction – diffusion" systems make the basis for modelling of such spatially distributed entities [3–16]. Famous Soviet mathematician Andrew Kolmogorov studied in detail such type of equations [17].

A reaction – diffusion methodology of modelling of spatially distributed populations faces a serious problem. Here the individual (behavioral) properties of organisms must be extremely specific and unfeasible: one must suppose that the organisms move over a space randomly and aimlessly [18, 19]. Obviously, such assumption almost never holds true (see, e.g. [20–22]), even for microorganisms [23–26]. The assumption towards the idle transfers of organisms in space is obviously less favorable for the species of higher taxonomy.

Modelling methodology based on evolution principles is the way to pass over the discrepancy mentioned above. This approach takes the origin from the evolution studies by J.B.S. Haldane [27]. This is the most general principle prescribing the way biological systems

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to evolve. In brief, it force to evolve a system toward the maximization of net reproduction. This latter is an average number of *per capita* descendants survived at the course of a series of reproductions over an arbitrary long generation line [28–32]. Later, they found this principle to be even more general, than just a biological one. Indeed, the principle holds true for any system where the inheritance takes place [33–39].

A consistent and efficient implementation of this principle faces the problem of a lack of knowledge of how the specific biological issues impact the survival of a species. In turn, the question arises, what is an entity to be evolving? An ordinary answer on this question is that the species is an evolving entity. Actually, the situation looks more complicated; not discussing this problem in detail, further we shall follow this idea. The principle formulated above yields the following rule for the model implemented below: evolution optimality in spatial distribution of organisms is equivalent to the maximization of (an average) net reproduction over space, with respect to the evolution trade off for such redistribution. Some further details on this issue could be found in [28, 30, 38, 40].

Here we present a very simple model of the dynamics of spatially distributed population that is based of the evolution optimality principle, rather than on a chemical kinetics similarity. The model is hardly expected to make some specific forecasting of a peculiar biological system. On the contrary, the model basically aims to figure out some important issues and effects in the dynamics that are definitely related to the targeted migration. The model makes a basis for further development in modelling of spatially distributed populations based on the evolution optimality principle. Such extensions and generalizations are discussed in Section 4.

1. Basic model of the smart migration

Consider a population inhabiting two stations; hence, the population consists of two subpopulations. Any movements of individuals within a station must be neglected; thus, only the transfer from station to station is considered as a migration act. No spatial effects in the population dynamics are presumed, for each subpopulation, as soon as no migration occurs.

We shall consider the model in discrete time t; the model is also discrete in space, i. e. a population is supposed to inhabit only two stations, and the transfer between these two stations affects the dynamics. This assumption comes from technical constraints, rather than from essential ones; a duality of discrete vs. continuous modelling is well discussed in literature, and we shall not intrude the discussion with the model. We shall deal with the model discrete both in time and space, and the pursued approach follows from technical reasons only, with neither respect to biological issues standing behind the implementation of continuous or discrete models.

The dynamics of each subpopulation is supposed to follow the Verhulst's equation [41–46]. Let N_t and M_t are the abundance of the first subpopulation (of the second one, respectively), so that

$$N_{t+1} = a \cdot N_t - b \cdot N_t^2 \tag{1a}$$

and

$$M_{t+1} = c \cdot M_t - d \cdot M_t^2 \,, \tag{1b}$$

respectively, in the migration-free case. Here a and c represent fertility at the relevant subpopulation, while b and d show the effect of density dependent competition within a subpopulation. It must be said, that unlike for the Verhulst's equation of a single population, one may not change the equations (1a, 1b) for the dimensionless form $\dot{x} = ax(1-x)$, eliminating the coefficients b and d, if migration runs. The point is that the migration effects would break down such transformation. The functions

$$k_r(N_t) = a - b \cdot N_t \tag{2a}$$

and

$$k_l(M_t) = c - d \cdot M_t \tag{2b}$$

are the net reproduction, in relevant stations, respectively.

Migration is a transfer of a part of subpopulation from one station into the other. Migration itself affects the reproduction, survival and other vital functions of an organism. All these issues will be integrated into the parameter called the *cost of migration* p: no negative impact on the reproduction, survival and other vital functions of an organism is observed, as $p = 1$. Otherwise, a decrease of p yields a decay in survival of organisms. Cost of migration p, $0 < p \leqslant 1$ may be considered as a probability of the successful transfer from station to station, i. e., with no damages for further reproduction [47–49]; see Fig. 1.

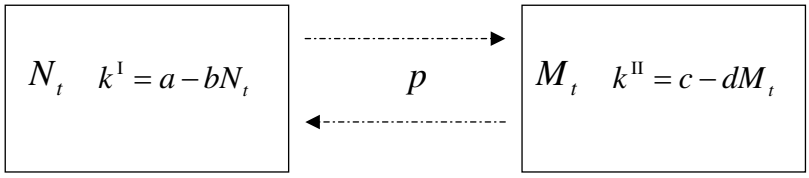

Fig. 1. Draft of the simplest model of optimal migration. k^{I} and k^{II} are the net reproduction in relevant stations. Dotted lines show the migration fluxes

Migration starts, as soon as the life conditions "there" become better than "here"; of course, with respect to the migration cost. The life conditions are measured in parts of net reproduction (2). This narrative could be easily formalized. Migration from N-station (from M-station, respectively) starts, if

$$p \cdot k_l(M) > k_r(N) \qquad (\text{if } k_l(M) < p \cdot k_r(N)\,, \text{ respectively})\ ,$$

for the given time moment t, $t = 1, 2, 3, \ldots$. The migration is supposed to run in a single act, entirely, and the reproduction always follows the migration. Thus, a life cycle of a population consists of two stages: the former is a migration (if it takes place at the given time moment t), and the latter is the reproduction ran according to (1), with the abundances upgraded due to migration. The reproduction runs at each station, independently.

Schematically, the model works in three steps.

The first step consists in the determination of the fact of migration, i.e. in the comparison of reproduction coefficients "there" and "here":

if	$p \cdot k_l(M)$	$>$ $k_r(N)$,	then the migration runs from N-station to M-station;
if	$k_l(M)$	$<$ $p \cdot k_r(N)$,	then the migration runs from M-station to N-station;
otherwise			no migration takes place.

The second step consists in the determination of the migration flux. Migration improves the life conditions measured in parts of net reproduction (2). An emigration results in the growth of that latter; reciprocally, immigration results in decrease. Of course, this clear and simple relations follows from linearity of the dependence of net reproduction (2) on the abundance N (or M). The migration flux tends to equalize the net reproductions, due to the abundance redistribution:

$$k_l(M - \Delta) = p \cdot k_r(N + p \cdot \Delta)$$

for the case of migration from M-station to N-station, and vice versa:

$$p \cdot k_l(M + p \cdot \Delta) = k_r(N - \Delta)\ .$$

Here the term $p \cdot \Delta$ represents the fact of mortality of individuals at the course of migration. The migration flux, then, is determined according to

$$\Delta_{MN} = \frac{pc - a + bN - pdM}{b + p^2 d} \tag{3a}$$

for the migration from N-station to M-station, and

$$\Delta_{NM} = \frac{pa - c + dM - pbN}{d + p^2 b} \tag{3b}$$

for the inverse migration. Of course, the number of emigrants may not exceed the number of habitants. This constraint makes the final formula for migration flux the following:

$$\Delta_{MN} = \min \left\{ N_t,\ \frac{pc - a + bN_t - pdM_t}{b + p^2 d} \right\} \tag{4a}$$

or

$$\Delta_{NM} = \min \left\{ M_t,\ \frac{pa - c + dM_t - pbN_t}{d + p^2 b} \right\} . \tag{4b}$$

Finally, **the third step** consists in the reproduction of organisms in both subpopulations independently, with respect to the upgraded abundance ($\widetilde{N}_t$, or $\widetilde{M}_t$, respectively) resulted from the migration:

$$N_{t+1} = a \cdot \widetilde{N}_t - c \cdot \widetilde{N}_t^2 \tag{5a}$$

and

$$M_{t+1} = c \cdot \widetilde{M}_t - d \cdot \widetilde{M}_t^2 . \tag{5b}$$

If no migration takes place for some time moment t, then $\widetilde{N}_t = N_t$ ($\widetilde{M}_t = M_t$, respectively). The formal algorithm of the model is shown in Fig. 2. This draft do not show a cycle.

Migration maximizes the average net reproduction determined over two stations. Let, for example, N^* and M^* be the figures providing that $k_r(N^*) = a - bN^*$ is less than $p \cdot k_l(M^*)$:

$$a - bN^* < p \cdot (c - dM^*) .$$

Then, targeted migration yields the maximization of the net reproduction; indeed, let Δ be the migration flux determined according to (3). It means that

$$a - b\,(N^* - \Delta) = p \cdot [c - d\,(M^* + p \cdot \Delta)] ,$$

where Δ is positive. Let, the compare the average (over two stations) net reproduction before migration, and after it. So, before migration average net reproduction is equal to

$$\frac{a - bN^* + c - dM^*}{2} .$$

The migration changes $a - bN^*$ for $a - (N^* - \Delta) = a - bN^* + b\Delta$ and $c - dM^*$ for $c - d(M^* + p\Delta) = c - dM^* - pd\Delta$. Then, average net reproduction becomes equal to

$$\frac{a - bN^* + c - dM^*}{2} + (b - pd)\Delta .$$

Here the additional term is positive, since b, d, p and Δ are not independent, and positivity of Δ requires the positivity of $b - pd$.

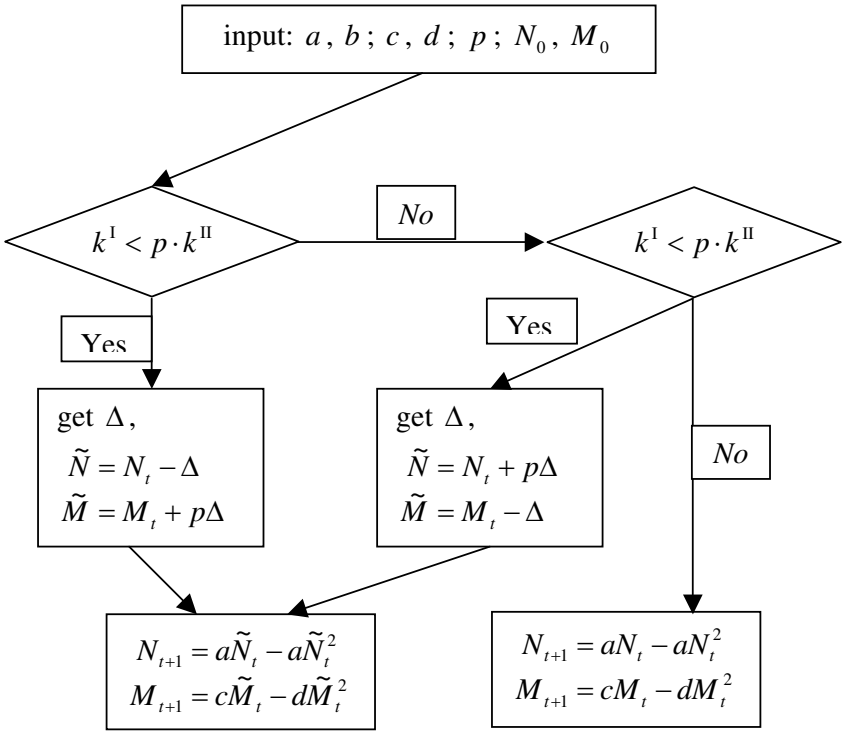

Fig. 2. Draft of the algorithm of the model (1 – 5). No recurrence is shown in the draft

2. Some properties of the model

To begin with, the model (1 – 5) is irreversible in time. This point differs it from any other known models of the dynamics of biological communities. The irreversibility follows from the smart migration implementation; indeed, the migration is a projection (see Fig. 3). A set of points in $(N \times M)$ space located alongside the strait lines shown in Fig. 3 by arrows is projected into a single point laying at the line determined by the equity

$$\Delta_{NM} = 0 \qquad \text{or} \qquad \Delta_{MN} = 0\,,$$

respectively (see Eqs. 3a and 3b). These conditions cut off the "rest area" (i. e., the area where no migration takes place, if a trajectory gets into it, at the time moment t):

$$\begin{aligned} pc - a + bN - pdM &= 0 \\ pa - c + dM - pbN &= 0\,. \end{aligned}$$

Obviously, these two lines (shown in solid in Fig. 3) collapses into the line determined by the equation

$$a - c + dM - BN = 0\,,$$

as $p = 1$.

Classical model be P. [41] exhibits a limitation for abundance. Indeed, if a single subpopulation (say, the model (1a)) is considered, so that no migration is implemented, then the abundance may not exceed a/b value; otherwise, a population would be eliminated. This fact results in the

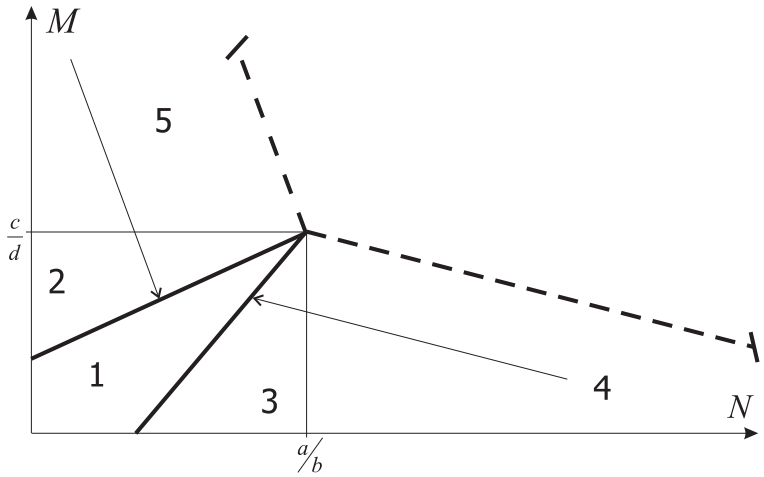

Fig. 3. Space available for the dynamic trajectories of the model, in case of non-zero migration; 1 — no migration area, 2, 5 — areas of migration from M-station to N-station, 3, 4 — areas of migration from N-station to M-station. Horizontal axis shows the abundance at N-station, vertical one shows similar abundance in M-station

parameter a constraint observed for the classical model: fertility factor a may not exceed 4. An excess of $a = 4$ would result in population elimination. Actually, a may exceed this value for classical model, while the dynamics will run in very specific Cantor set, that makes such dynamics unobservable [42, 43].

The smart migration extends both the parameters a and c levels, and the feasible abundances, in both stations. That latter is shown in Fig. 3 as swallow tail outlined by dashed lines. Evidently, the abundances in the stations are not independent: an excess of an abundance over the critical value of a/b (or c/d, respectively) may not take place simultaneously. If it happens, then the population is eliminated. Thus, the maximal abundance $N_{\max}$ ($M_{\max}$, respectively) in a station may be reached, when the opposite station is empty:

$$N_{\max} = \frac{c}{d} + \frac{a}{pb} \qquad \text{and} \qquad M_{\max} = \frac{c}{pd} + \frac{a}{b}\,.$$

The tangent of the dashed line bordering the area 5 is equal $-p^{-1}$; similarly, for the area 4 the tangent is equal to $-p$. The area 1 expands, as $p \to 0$ occupying the entire rectangular $[0, a/b] \times [0, c/d]$, for $p = 0$. The areas 4 and 5 become a (semi-infinite) strip each, of the permanent width. This fact differs the situation of the complete absence of a migration from the infinitely big migration cost μ.

Equation (1a) (or (1b), respectively) exhibits various dynamic patterns, as parameter a (or parameter c, respectively) varies [4, 5, 10, 41–44, 46]. The limit regime of (1) varies from a stable fixed point to a strange attractor. Similar diversity of regimes could be found at the equation system (1a, 1b), when the migration occurs. Obviously, the system (1 – 5) exhibits some other regimes, peculiar for smart migration models.

3. Some simulation results of the dynamics of targeted migration

Targeted migration yields a connection in the dynamics of two (formerly independent) subpopulations. Thus, the dimension of the system increases, in comparison to the classical model. It makes the analytical solution (and analysis) of possible limit regimes very hard, if feasible. Here the simulation makes sense; Figs. 4 – 7 show various limit regimes observed for the model (1 – 5), in simulations.

Fig. 4 shows the periodical dynamics in the model (1 – 5). This figure presents the dynamics observed for the perfect mobility of individuals, i. e., with $p = 1$. Slow resolution of the figure

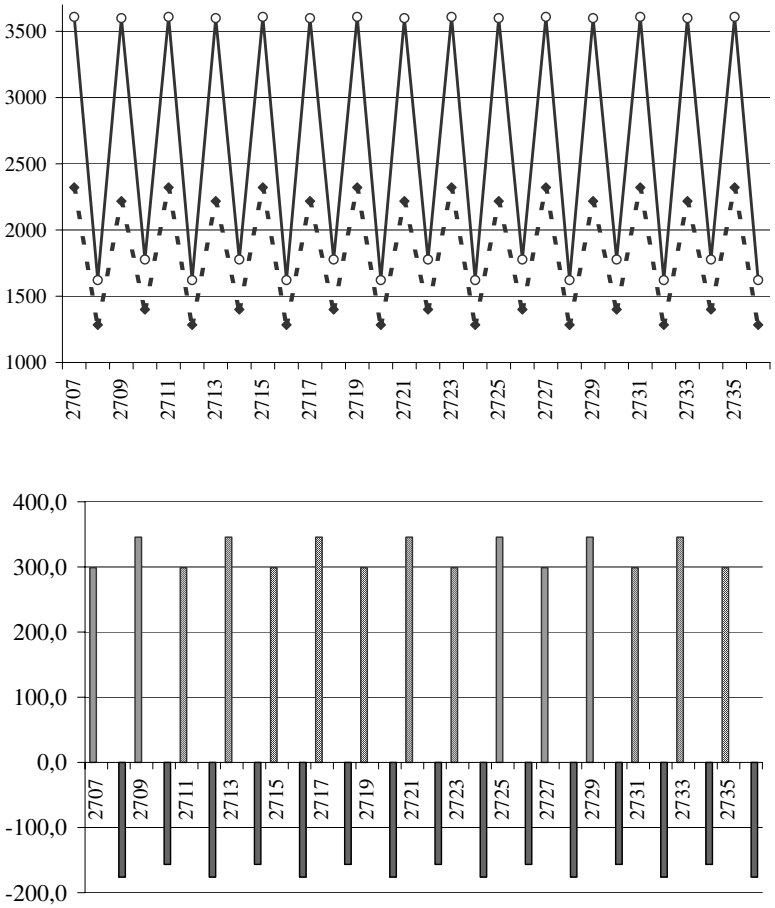

Fig. 4. Cyclic dynamics of the population with smart migration. The cycle length of the oscillations of abundances (upper draft) in stations and migration fluxes (lower draft) is 4; the parameters are $a = 3.11$ (dashed line), $c = 3.8$ (solid line), $b = d = 0.001$

masks the periodicity: the abundances are 2321.1, 1283.8, 2218.1 and 1400.3 at the station I; the relevant values for the station II are 3608.9, 1621.9, 3599.6 and 1777.1, respectively. The lower draft at Fig. 4 shows the migration fluxes. Evidently, the number of migrating beings is positive; we have denoted the opposite migrations with positive and negative signs, respectively.

To examine the effect of non-zero transfer cost on the dynamics, we have simulated the

dynamics of the model with the same parameters values, and $p = 1/2$. It has several rather surprising effects. First of all, a highly ordered limit regime is changed with the complex non-periodic dynamics. Next, a total abundance of the population increased. Average abundances in the stations are 1805.8 and 2651.9, for $p = 1$; it makes the total abundance equal to 4457.7. The corresponding values are 2038.7 and 2487.5 making the total abundance equal to 4526.3, for $p = 1/2$; Fig. 5 illustrates this change.

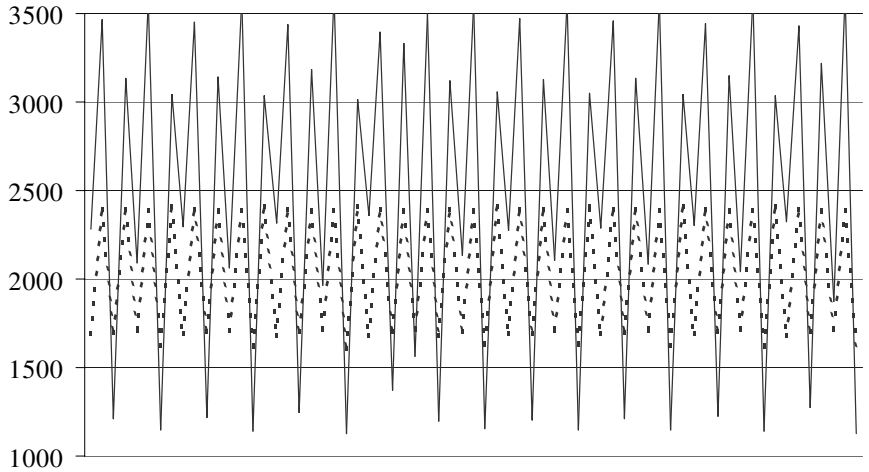

Fig. 5. Complex dynamics observed for the same parameters values, as in Fig. 4; denotations are the same, as well, but $p = 1/2$

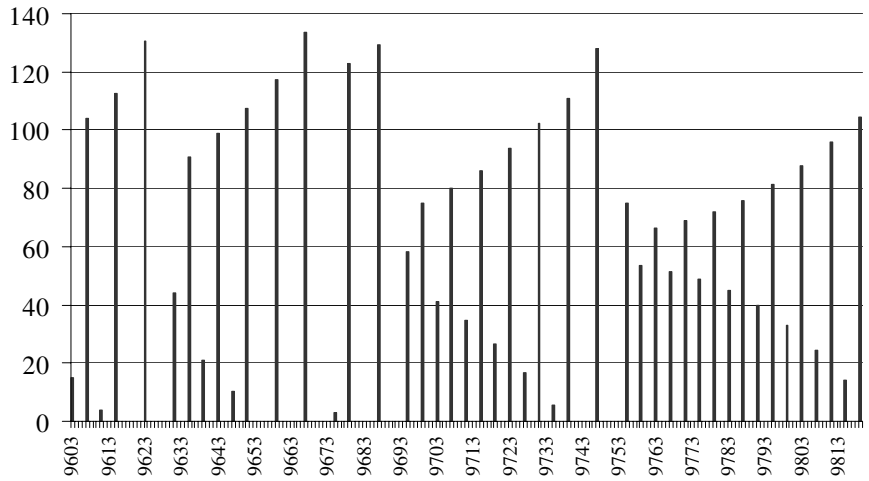

Fig. 6. One-way migration observed at the model with parameters indicated in Fig 4, for $p = 1/2$

Also, the pattern of migration fluxes has changed completely. To begin with, the regular and rather simple pattern of migration observed for the indicated parameters with $p = 1$ is changed for complex, even chaotic like pattern, as $p = 1/2$ (see Fig. 6). There is no any periodicity in the migration occurrence, at all. The migration runs accidently, in some time moments; there are no permanent fluxes observed each time moment. One hardly could claim the migration acts to be random, while their pattern seems to be quite chaotic. The diversity of limit regimes observed in the model is quite abundant; moreover, the regimes are controlled

with several (five, to be exact) parameters, and there is no evident way to decrease the number of parameters determining the dynamics of the model. Such actual dependence of the model on several parameters makes the analysis of limit regimes, and their transformations very hard problem. Table 1 illustrates the impact of fertility factor on the evolutionary advances of smart migration, in two cases of transfer cost: $p = 1$ and $p = 1/2$.

Table 1. Average subpopulation abundance $\langle N \rangle$ and $\langle M \rangle$ in each station observed for various levels of fertility factor (Malthusian parameter) c in a station. Parameters $a = 1.11$, $b = d = 0.001$ were permanent, for all cases; the variation of parameter c is shown in the table.

	$p = 1$		$p = 1/2$			$p = 1$		$p = 1/2$	
c	$\langle N \rangle$	$\langle M \rangle$	$\langle N \rangle$	$\langle M \rangle$	c	$\langle N \rangle$	$\langle M \rangle$	$\langle N \rangle$	$\langle M \rangle$
4.85	45.8	2991.1	45.8	3104.5	4.25	147.0	3075.4	112.2	2987.2
3.70	110.1	2699.9	98.1	2462.3	4.87	110.5	3847.9	104.5	3429.7
3.95	110.1	2949.8	81.6	2729.8	5.05	0.1	2.6	92.7	3647.8
4.15	151.1	3029.0	103.1	2903.4					

Finally, Fig. 7 shows the regime with soft loss of stability of migration. The curves in the figure are evidently separated in two part: the former is a smooth dynamics running for quite a time, and the latter is an abrupt chaos-like oscillation regime. This regime itself makes no matter of interest; a migration pattern is interesting here. The point is, that for quite a long

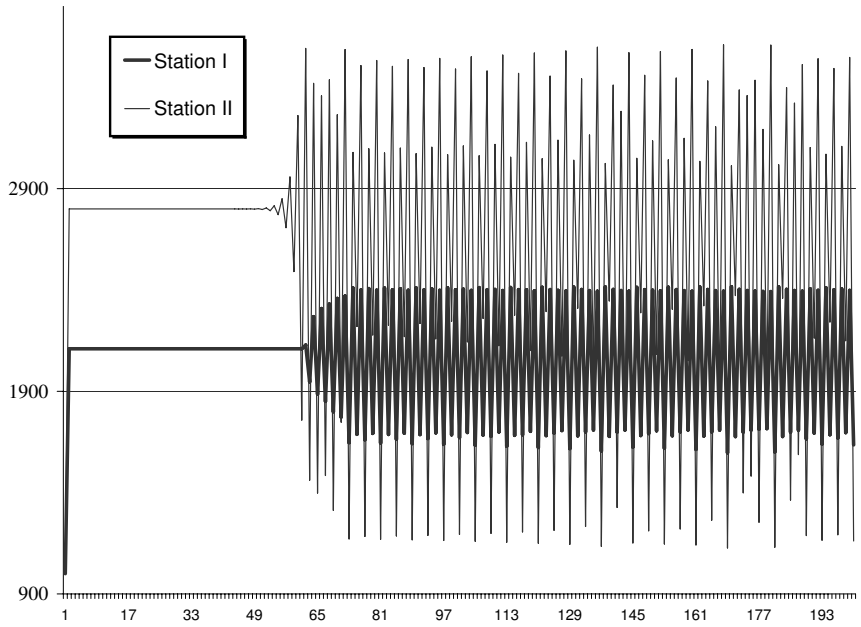

Fig. 7. Slow loss of stability

time, there is no migration. Then, due to a complex dynamics observed within a station, a migration starts. The migration causes an instability of the oscillatory regime in both stations, so that the magnitude of those oscillation grows drastically. stations).

4. Discussion

Here we present the simplest model of a smart migration, strongly opposing the "reaction – diffusion" methodology. The model is rather clear and apparent. It is presented by a cascade (discrete time dynamic system) with discontinuity; this latter results from the targeted migration. The targeted migration is a projection resulted from the idea of maximization of an overall net reproduction (in average, over two

Apparently, the model (1 – 5) brings serious technical or mathematical problems, at least, for the analysis of limit regimes transformations (bifurcations, etc.). On the other hand, the proposed model makes no problems for simulations and numerical analysis. Here we shall not turn onto the discussion of the mathematical issues of the model, but consider some biological issues standing behind it.

To begin with, this is the model of globally informed individuals. An idea of the information (or knowledge, to be exact) standing behind the decision towards a migration act made by a being is not so simple and facile. Quite a few is known towards the spatial behaviour of various species; yet, a lot is still conspired from a researcher. Thus, the knowledge controlling the spatial behaviour, as well as the information affecting that latter is the matter to be discussed properly. Apparently, these issues must be discussed each time *de novo*, when a model of spatial dynamics is considered.

Indeed, an individual makes a decision whether to migrate, or remain staying in the station, referring to the available information concerning the life conditions. So, the key issue is what information towards that matter is available. In general, there could be three options: **global accessibility** of information or knowledge; **local accessibility** of them, and **complete inaccessibility** of these former.

The model (1 – 5) presumes, that the beings have the **global accessibility** to all the necessary information concerning the decision on a migration act, as well as the relevant knowledge. In reality, a migration act seems to be rather complex phenomenon controlled by numerous mechanisms and affected with a number of factors; they could be separated into two classes. The former are the environmental (or external, more generally) factors, while the latter are the individual (or inner, in general) ones. Definitely, the factors from different classes may interact and be rather dependent; meanwhile, such classification brings some transparency into the problem.

Environmental conditions are those determined by the external medium; a list of them might be rather long, say, food and shelter availability, insolation, temperature, salinity, humidity, predation or harvesting stress, intraspecific competition and interspecific competition, etc. Surely, the list may be extended.

Inner conditions are those determined by the individual features of a being. Size, weight and age come the first. Experience and acquaintance to a habitation site are also important. A diversity of strategies in fighting and conflict interactions should also be included into the list. A satiation vs. starvation are also important. Presence of off-spring, as well as the strategies of the off-spring care must not be neglected, etc.

The model (1 – 5) provides that all the diversity of the life conditions at any station are converted into a couple of parameters a and b (c and d, respectively). The global accessibility, then, means that the beings know these four parameters, to make a decision towards the migration. Besides, it is supposed that the density of the subpopulation (or its total abundance N, or M, respectively) is known, as well. Not discussing at the moment the details of the detection of population density, or other conditional parameters *per se*, suppose that the environmental abundance (density, indeed) and other parameters are detectable for an individual. A feasibility of such presumption may be argued, while it is a common place for mathematical population biology [7, 8, 11, 18, 46, 50–52].

Definitely, the global information access means also the knowledge of the transfer cost from a station to another one, and back. Again, we shall not discuss in details the biological feasibility

of such assumption. It should be implemented into a model, if one tends to model a dynamics within the global information accessibility approximation.

The local accessibility means that the beings have a limited access to the information and knowledge mentioned above. The limitations may differ in nature, while they should be described explicitly. The problem here is that there is no clear way to figure out information or knowledge to be excluded from the access. Nevertheless, there are some approaches seeming rather natural. Quite obvious, that one may exclude the knowledge on the environmental conditions at the station of immigration. The lack of this knowledge seriously changes the migration conditions (3a, 3b). Alternatively, a migration may have a threshold pattern: immigration starts, as soon, as the abundance in the habitat station exceeds some given level, say:

$$\Delta_{MN} = \max\left\{0,\ N - \frac{a}{2b}\right\} \tag{6a}$$

or

$$\Delta_{NM} = \max\left\{0,\ M - \frac{c}{2d}\right\}\ . \tag{6b}$$

Here the threshold abundance is supposed to be equal to the maximal off-spring number, in the next generation. Another option to model a local information accessibility is to restrict the knowledge of the transfer cost p; we shall not discuss these issues in more detail (see, e. g., [53]). The local accessibility of information and/or knowledge may result in the migration running in opposite directions, simultaneously.

The methodology presented above is rather powerful, and provides a researcher with the tool to study spatially distributed communities keeping beyond the artificial and absolutely unrealistic hypotheses on the microscopic behavior of individuals, i.e. the randomness and aimlessness of their transfers over a space. The model described above (see Section 1.) could be extended for the case of two-species (or several species) community dynamics, with optimal migration. Obviously, a two-station model describing a dynamics of two-species (say, predators and preys) or several species community who get a global accessibility to the information or knowledge necessary for optimal migration seems to be the simplest one. A dynamics within a station might be modeled with the most common equation (say, Lotka-Volterra equation), thus explicating the effect of smart migration in the dynamics of a multi-species community.

A study of multi-species community dynamics due to the version of the model of optimal migration (1 – 5) brings some peculiar issues into consideration. As soon, as a competitive interaction is considered, one has to take into account a possibility of the implementation of reflexive behaviour. In particular, a reflexivity may take place in the spatial distribution resulted from the evolution optimality principle.

Another significant constraint of the model (1 – 5) is the spatial structure limited with two stations. Indeed, an expansion of the approach presented above for the case of several stations, and, ultimately, for a continuous, or quasi-continuous case of a habitat is strongly desirable. Suppose, a population inhabits three stations. Again, here we presume the global information accessibility, as well. Suppose, further, the conditions (i.e., the abundances and the parameters) yield the situation when the individuals from the station A must migrate either to station B, or to station C. No one knows exactly, in advance, what is a proportion of individuals immigrating into the station B vs. those immigrating the station C. This is the main obstacle here. There exists the approach withdrawing this discrepancy; it is based on the interval mathematics [54–58]. The detailed discussion of that issue falls beyond the scope of this paper.

5. Conclusion

The model described above implements the methodology of evolution optimality into the problem of the modelling of spatially distributed populations. Migration causes the maximization

of net reproduction (which is a reproduction rate, in our case), in average, over the space. The model comprises the simplest case of two stations, where the spatial distribution is restricted to a transfer of individuals from station to station and back; the transfer cost is supposed to be symmetrical one. The model shows the expansion of the environment capacity, in comparison to the case of the migration absence.

The main purpose of this paper is to show the methodology of the modelling of spatially distributed populations (and other biological communities) with no chemical analogies, rather than to find out some peculiar dynamic regime pretending to match exactly a dynamics of a real biological community.

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Простейшая модель целенаправленной миграции

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Рассмотрена простейшая модель оптимизационной миграции глобально информированных особей. Рассмотрены различные предельные режимы, обсуждена проблема определения их устойчивости.

Ключевые слова: отбор, максимизация, коэффициент размножения, цена перемещения, проекция.